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Microbial Growth in a Plug Flow Reactor with Wall Adherence and Cell Motility

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1. INTRODUCTION

In a recent series of papers [3, 4], a model of microbial competition for limiting nutrient and wall space in a plug flow reactor was investigated using analytical and numerical techniques. A key feature of the model, first formulated for the chemostat (viewed as a surrogate for the large intestine) by Freter [6–8], is that bacteria are assumed to be capable of attachment to the wall of the reactor, forming a biofilm, from which they are relatively protected against washout from the reactor. In these earlier models, the wall-attached bacteria were assumed to be immobile, in contrast to the free bacteria (those in the bulk fluid compartment) which were assumed to be randomly motile. Of course, the assumption that wall-attached bacteria are immobile is an approximation and it turns out this approximation is not a simplification. A mathematical consequence of the assumed immobility of the wall-attached bacteria is that the equation describing the areal density of wall-attached bacteria is an ordinary differential equation with spatial parameter whereas the equations describing the limiting nutrient and the free bacterial density are reaction-advection-diffusion equations. Due to the absence of the compactifying diffusion term in this one equation, we were unable to prove the existence of a compact attractor for the dynamics of the system as a whole although we conjecture that a compact attractor exists. The mathematical analysis in [4] was limited and made more difficult by this lack of compactness. Therefore, it seems natural to drop the assumption that wall-attached cells are

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immobile in favor of the assumption of a relatively small, but nonzero, random motility (i.e., diffusivity). By choosing Neumann boundary conditions at both ends of the reactor for the wall-attached bacteria, we retain the feature of the original model that wall-attached cells are immune from washout (unless they are sloughed off the wall). Thus, the modified model essentially retains the biological meaning of the orignal one and at the same time becomes more tractable to mathematical analysis.

We can establish the existence of a compact attractor for the system and this allows the use of powerful results on uniform persistence and permanence, developed by Hale and Waltman [10], Hutson and Schmitt [11], Thieme [20], and Zhao [21]. See also the appendix in [18] for a result on uniform persistence uniform with respect to parameters. In fact, in an appendix to this paper, we significantly extend the robust persistence results in [11, 18, 22]. The existence of a positive equilibrium solution of the model system, representing the survival of the bacterial population in the reactor, then follows at once from uniform persistence and the existence of the compact attractor (see [21]).

Our results have the following biological implications. We identify two possibilities for a bacterial population capable of wall attachment in the plug flow reactor. Either the reactor environment is not favorable for growth and the bacteria are ultimately washed out or the population is capable of growing at a rate sufficient to offset washout and the population persists in the reactor and there exists at least one positive steady solution with organisms present. While we conjecture that the two regimes are distinguished by the sign of a single dominant eigenvalue (for the linearization about the washout steady state), we are unable to prove such a sharp result. If the washout steady state is unstable in the linear approximation, we show that the bacterial population survives while if a somewhat stronger condition than asymptotic stability of the washout steady state holds, then washout of the organism occurs.

In the next section, we briefly describe the modified model. For more details on the modeling, see [3]. We next prove that the resulting strongly coupled parabolic system possesses a compact attractor in the space of continuous functions. The latter follows fairly standard lines (see [12–14]). Subsequent sections examine the stability properties of the trivial washout steady state and establish the uniform persistence of the bacterial population and the existence of a nontrivial steady state. An appendix contains a very useful result on so-called robust persistence. Whereas uniform persistence theory, in the present context, shows that the maximum norm of the bacterial density eventually exceeds an initial-condition independent, positive quantity, robust persistence asserts that the minimum bacterial density has the same property. Since the total biomass is the integral of the bacterial density, the latter assertion allows us to truly say that the bacterial population persists.

2. THE MODEL

Consider a long thin tube with circumference C and cross-sectional area A extending along the x-axis. The reactor occupies the portion of the tube from $x = 0$ to $x = L$. It is fed with growth medium at a constant rate at $x = 0$ by a laminar flow of fluid in the tube in the direction of increasing x and at velocity v (a constant). The external feed contains all nutrients in near optimal amounts except one, denoted by s, which is supplied in a constant, growth-limiting concentration S^0. We allow the possibility that the feed contains bacteria at constant concentration u^0 although the case that $u^0 = 0$ will be of primary interest. The flow carries medium, depleted nutrients, cells, and their byproducts out of the reactor at $x = L$. Nutrient S is assumed to diffuse with diffusivity d_0, free microbial cells are assumed to be capable of random movement, modeled by diffusion with diffusivity (sometimes called random motility coefficient) d, and wall-attached bacteria are assumed to undergo random motion on the wall surface which is modeled by diffusion with diffusivity d_1. We assume negligible variation of free bacteria and nutrient concentration transverse to the axial direction of the tube.

The model accounts for the density of free bacteria (bacteria suspended in the fluid) $u(x,t)$, the density of wall-attached bacteria $w(x,t)$, and the density of nutrient $S(x,t)$. The total free bacteria at time t is given by

$$A\int_0^L u(x,t)\,dx$$

and the total bacteria on the wall at time t is given by

$$C\int_0^L w(x,t)\,dx.$$

The quantities S, u, w satisfy the following system of equations,

$$\begin{aligned}
S_t &= d_0 S_{xx} - vS_x - \gamma^{-1}uf(S) - \gamma^{-1}\delta w f_w(S),\\
u_t &= du_{xx} - vu_x + u(f(S) - k) + \delta w f_w(S)(1 - G(W))\\
&\qquad - \alpha u(1 - W) + \delta\beta w,\\
w_t &= d_1 w_{xx} + w(f_w(S)G(W) - k_w - \beta) + \alpha\delta^{-1}u(1 - W),
\end{aligned} \tag{2.1}$$

with boundary conditions

$$\begin{aligned} vS^0 &= -d_0 S_x(0,t) + vS(0,t), \qquad S_x(L,t) = 0, \\ vu^0 &= -du_x(0,t) + vu(0,t), \qquad u_x(L,t) = 0, \\ 0 &= w_x(0,t) = w_x(L,t), \end{aligned} \tag{2.2}$$

and initial conditions

$$S(x,0) = S_0(x), \qquad u(x,0) = u_0(x), \qquad w(x,0) = w_0(x), \qquad 0 \le x \le L. \tag{2.3}$$

Some remarks concerning the boundary conditions may be useful here since there is a possibility of confusion. The flux of nutrient S or free bacteria u out either end of the reactor consists of a sum of two parts, advection and diffusion. Thus, the boundary conditions $S_x = 0$ (or $u_x = 0$) at $x = L$ means that the flux out is entirely due to advection; it does **not** mean that the flux out is zero. On the other hand, the wall-attached bacteria are assumed not to feel the flow (technically, v should vanish on the wall surface anyway) so the boundary conditions $w_x = 0$ at both ends means that there is no flux of wall-attached bacteria out of the reactor at either end.

The nutrient uptake rates for free and wall-attached bacteria are given by functions f and f_w, assumed to satisfy

$$f \in C^1, \qquad f(0) = 0, \qquad f'(S) > 0.$$

A typical example is the Monod function

$$f(S) = \frac{mS}{a + S}.$$

It is assumed that there is a finite upper bound w_∞ on the density of available wall sites for colonization. The fraction of daughter cells of wall-bound bacteria finding sites on the wall, $G(W)$, as a function of the occupancy fraction $W = w/w_\infty$ is assumed to satisfy

$$G \in C^1, \qquad 0 < G(0) \le 1, \qquad G'(W) < 0, \qquad G(1) = 0.$$

Freter et al. [6–8] use

$$G(W) = \frac{1 - W}{a + 1 - W},$$

where a is typically very small.

Free bacteria are attracted to the wall at a rate proportional (with constant α) to the product of the free cell density u and the fraction of available wall sites $1 - W$. Finally, we assume that wall-attached cells are sloughed off the wall by mechanical forces proportional to their density. Except where explicitly mentioned, all parameters appearing in the model are assumed to be positive except possibly the cell death rates $k \geq 0$ and $k_w \geq 0$, which are sometimes ignored. See [3] for further details on the modeling.

In [4], system (2.1) is considered with $d_1 = 0$ and the boundary condition for w is dropped.

Suitable dimensionless variables and parameters are summarized below:

$$\bar{S} = S/S^0, \qquad \bar{u} = u/\gamma S^0, \qquad \bar{u}^0 = u^0/\gamma S^0, \qquad \bar{w} = W = w/w_\infty,$$

$$\bar{x} = x/L, \qquad t = vt/L, \qquad d_i = d_i/Lv, \qquad \bar{d} = d/Lv,$$

$$\bar{f}_w(\bar{S}) = (L/v)f_w(S^0\bar{S}), \qquad \bar{\alpha} = (L/v)\alpha, \qquad \bar{\beta} = (L/v)\beta,$$

$$\bar{k} = (L/v)k, \qquad \bar{k}_w = (L/v)k_w, \qquad \bar{f}(\bar{S}) = (L/v)f(S^0\bar{S}).$$

Define

$$\epsilon = \frac{\delta w_\infty}{\gamma S^0}.$$

Then, in terms of these quantities, the model equations (2.1)–(2.2) become, on dropping the overbars,

$$\begin{aligned} S_t &= d_0 S_{xx} - S_x - uf(S) - \epsilon w f_w(S), \\ u_t &= du_{xx} - u_x + u(f(S) - k) + \epsilon w f_w(S)(1 - G(w)) \\ &\quad - \alpha u(1 - w) + \epsilon\beta w, \\ w_t &= d_1 w_{xx} + w\big(f_w(S)G(w) - k_w - \beta\big) + \epsilon^{-1}\alpha u(1 - w), \end{aligned} \tag{2.4}$$

with boundary conditions

$$\begin{aligned} 1 &= -d_0 S_x(0,t) + S(0,t), \qquad S_x(1,t) = 0, \\ u^0 &= -du_x(0,t) + u(0,t), \qquad u_x(1,t) = 0, \\ 0 &= w_x(0,t) = w_x(1,t), \end{aligned} \tag{2.5}$$

and initial conditions

$$S(x,0) = S_0(x), \qquad u(x,0) = u_0(x), \qquad w(x,0) = w_0(x), \qquad 0 \leq x \leq 1. \tag{2.6}$$

3. EXISTENCE OF A COMPACT ATTRACTING SET

Let C denote the Banach space of continuous real-valued functions on $[0,1]$ with the uniform norm, $\|\cdot\|$, and $C^3 = C \times C \times C$. The initial data are assumed to belong to the set $X = \{(S_0, u_0, w_0) \in C^3\colon S_0 \geq 0,\ u_0 \geq 0,\ 0 \leq w_0 \leq 1\}$. Our first result says that the initial boundary value problems Eqs. (2.4)–(2.6) is well-posed as a dynamical system on X. More formally, the map Φ defined by

$$\Phi(t)(S_0, u_0, w_0) = (S(\cdot, t), u(\cdot, t), w(\cdot, t)),$$

where $(S(x,t), u(x,t), w(x,t))$ is the solution of Eqs. (2.4)–(2.6), is continuous on $X \times [0, \infty)$ into X and satisfies $\Phi(0) = id_X$ and the semigroup property $\Phi(t)\Phi(s) = \Phi(t+s)$ for $t, s \geq 0$. Furthermore, Φ is dissipative in the L^1 sense so that there is a finite ultimate upper bound on the biomass that can be supported in the reactor by the nutrient in the feed stream which is independent of the initial data. It is a first step towards establishing the existence of a global attractor.

PROPOSITION 3.1. *The system Eqs.* (2.4)–(2.6) *induces a semidynamical system on X. In particular,* $0 \leq w(x,t) \leq 1$ *for all* (x,t). *Moreover, if* $\beta + k_w > 0$, *then there exists* $M > 0$, *independent of the initial conditions, such that for every solution of Eqs.* (2.4)–(2.6), *we have*

$$\limsup_{t \to \infty} \int_0^1 u(x,t)\, dx \leq M. \tag{3.1}$$

Finally, there exists $\sigma, C > 0$, *independent of initial data, such that*

$$\|S(\cdot, t)\| \leq 1 + C\|S_0\| e^{-\sigma t}.$$

Proof. For each $(S_0, u_0, w_0) \in X$, the existence of a unique solution (S, u, w) of Eqs. (2.4)–(2.6) defined for all $t \geq 0$ and belonging to X for each fixed t can be argued exactly as in [3] using [16, Theorem 7.3.1]. Global existence follows from comparison of the solution with that of an associated linear system as in [3].

Now we turn to the L^1 estimate of u. The eigenvalue problem

$$\begin{aligned} \lambda\phi &= d\phi'' - \phi', \\ 0 &= -d\phi'(0) + \phi(0), \qquad \phi'(1) = 0, \end{aligned} \tag{3.2}$$

plays a fundamental role here. Its eigenvalues, $\{\lambda_n\}_{n \geq 0}$, satisfy (see [2]) $\lambda_{n+1} < \lambda_n$, and $\lambda_0 < -1$. In order to emphasize the dependence of λ_n on d, we sometimes write $\lambda_n(d)$ and, to take account of the sign of the dominant eigenvalue, we define $\lambda_0 = -\lambda_d$.

Let $\psi_d > 0$ be the principal eigenfunction of the Sturm–Liouville problem adjoint to Eq. (3.2),

$$\begin{aligned} \lambda\psi &= d\psi'' + \psi', \\ 0 &= d\psi'(1) + \psi(1), \qquad \psi'(0) = 0, \end{aligned} \tag{3.3}$$

corresponding to the eigenvalue $-\lambda_d$. We normalize ψ_{d_0} by requiring $\psi_{d_0}(0) = 1$ and normalize ψ_d by requiring that $\psi_d(x) \le \psi_{d_0}(x)$, $0 \le x \le 1$, with equality holding for some x. Define

$$X = \int_0^1 S(x)\psi_{d_0}(x)\,dx, \qquad Y = \int_0^1 u(x)\psi_d(x)\,dx,$$

$$Z = \int_0^1 w(x)\,dx.$$

Multiplying the first equation of Eq. (2.4) by ψ_{d_0}, the second by ψ_d, and integrating all three equations, using the identity

$$\int_0^1 [du'' - u']v = (-du'(0) + u(0))v(0) + \int_0^1 u[dv'' + v'],$$

where u satisfies $u'(1) = 0$ and v satisfies the boundary conditions in Eq.(3.3), we get

$$\begin{aligned} X' &= 1 - \lambda_{d_0}X - \int_0^1 u\psi_{d_0}f - \epsilon\int_0^1 w\psi_{d_0}f_w, \\ Y' &= u^0\psi_d(0) - (\lambda_d + k)Y + \int_0^1 u\psi_d f + \epsilon\int_0^1 w\psi_d f_w(1-G) \\ &\quad - \alpha\int_0^1 u\psi_d(1-w) + \epsilon\beta\int_0^1 w\psi_d, \\ Z' &= \int_0^1 wf_wG - (k_w + \beta)Z + \epsilon^{-1}\alpha\int_0^1 u(1-w). \end{aligned} \tag{3.4}$$

If $Q = aX + mY + \epsilon Z$, where $m > 0$ and $a > 0$ are to be determined, then we get

$$\begin{aligned} Q' &\le a + mu^0 - \lambda_{d_0}aX - (\lambda_d + k)mY - (k_W + \beta)\epsilon Z \\ &\quad + \epsilon\int_0^1 wf_w\left[G + m(1-G)\psi_d - a\psi_{d_0}\right] + \epsilon m\beta\int_0^1 w\psi_d \\ &\quad + \int_0^1 uf\left(m\psi_d - a\psi_{d_0}\right) + \alpha\int_0^1 u(1-w)(1-m\psi_d), \end{aligned}$$

where we have used that $\psi_d(0) \le \psi_{d_0}(0) = 1$. Choose $a \ge 1$ to be minimal with the property that $1 \le a\psi_d$ and let $\alpha a/(\lambda_d/2 + k + \alpha) = m$. Since $a > m$ and $\psi_d \le \psi_{d_0}$, the third integral is nonpositive. Furthermore,

$$\begin{aligned} G - a\psi_{d_0} + m\psi_d(1 - G) &\le [aG - a + m(1 - G)]\psi_d \\ &= [(a - m)G + m - a]\psi_d \\ &\le (a - a)\psi_d = 0, \end{aligned}$$

so the first integral is nonpositive. As $m < a$, the set E where $1 - m\psi_d > 0$ has positive measure. The last integral may be estimated as follows.

$$\begin{aligned} \alpha\int_0^1 u(1 - w)(1 - m\psi_d) &\le \alpha\int_E u(1 - m\psi_d) \\ &\le \alpha\int_E u(a - m)\psi_d \\ &= -\alpha\left(1 - \frac{a}{m}\right)mY. \end{aligned}$$

The second integral is estimated using $w \le 1$ and $\psi_d \le \psi_{d_0} \le 1$, where the latter follows because $\psi_d' \le 0$. Putting these estimates together, we have

$$\begin{aligned} Q' &\le a + mu^0 + \epsilon m\beta - \lambda_{d_0} aX - \left[\lambda_d + k + \alpha\left(1 - \frac{a}{m}\right)\right]mY \\ &\quad - (k_w + \beta)\epsilon Z \\ &= a + mu^0 + \epsilon m\beta - \lambda_{d_0} aX - (\lambda_d/2)mY - (k_w + \beta)\epsilon Z \\ &\le a + mu^0 + \epsilon m\beta - LQ, \end{aligned}$$

where $L = \min\{\lambda_{d_0}, k_w + \beta, \lambda_d/2\}$. Hence,

$$\limsup_{t\to\infty}(aX + mY + \epsilon Z) \le L^{-1}\left(a + m\left(u^0 + \epsilon\beta\right)\right).$$

Finally, we note that

$$S_t \le d_0 S_{xx} - S_x,$$

so $N = S - 1$ satisfies the same differential inequality but with homogeneous boundary conditions. A standard comparison principle yields the final estimate. ∎

The main result of this section is that semidynamical system Φ, generated by system Eqs. (2.4)–(2.6), has a compact global attractor. We assume that $\beta + k_w > 0$ throughout the remainder of the paper.

THEOREM 3.2. *$\Phi(t)$ is completely continuous for each $t > 0$ and there exists a compact attractor A in X for Φ which attracts each bounded subset of X.*

Proof. The following L^∞ estimates are key. For each $R > 0$, there exists $B(R) > 0$ such that if $\|(S_0, u_0, w_0)\| \le R$,then $\|u(\cdot, t)\| \le B(R)$ for $t \ge 0$. There is a constant $C > 0$, independent of initial data, such that

$$\limsup_{t \to \infty} \| u(\cdot, t) \| \le C. \tag{3.5}$$

Both are obtained by a standard bootstrapping argument beginning with analogous estimates in the L^1 norm. These in turn follow from the proof of Proposition 3.1 and estimate (3.1). Using the linear growth bound of the reaction term in the u equation with respect to the u variable (due to the L^∞ boundedness of S and w), one can get corresponding L^p estimates for arbitrarily large p and ultimately L^∞ estimates. See, e.g., [12–14]. The complete continuity of Φ follows from the first estimate above and the compactness of the linear semigroup generated by the elliptic differential operators appearing in Eq. (2.4). The existence of a global attractor follows from Ref. (3.5) (which provides for point dissipativity) and from the complete continuity assertion. See [9, Theorem 3.4.8] and [13, Corollary 3.6]. ∎

4. STABILITY OF WASHOUT STEADY STATE

If there is no input of microorganisms from inflow, that is, if $u^0 = 0$, which we assume throughout this section, then the system Eqs.(2.4)–(2.6) has a trivial steady state

$$S \equiv 1, \qquad u = w \equiv 0,$$

which we refer to as the "washout steady state" since no organisms are present. Our goal in this section is to examine the stability properties of this steady state. The reason for focusing on this uninteresting steady state is that to find conditions for it to be unstable is to find conditions for a bacterial population to survive in the reactor.

The linearization of Eqs. (2.4)–(2.6) about the washout steady state is given by (we use the same variable names)

$$\begin{aligned} S_t &= d_0 S_{xx} - S_x - uf(1) - \epsilon w f_w(1); \\ u_t &= d u_{xx} - u_x + u(f(1) - k) + \epsilon w f_w(1)(1 - G(0)) \\ &\qquad - \alpha u + \epsilon \beta w, \\ w_t &= d_1 w_{xx} + w(f_w(1) G(0) - k_w - \beta) + \epsilon^{-1} \alpha u, \end{aligned} \tag{4.1}$$

with the homogeneous boundary conditions

$$0 = -d_0 S_x(0,t) + S(0,t), \qquad S_x(1,t) = 0,$$
$$0 = -du_x(0,t) + u(0,t), \qquad u_x(1,t) = 0,$$
$$0 = w_x(0,t) = w_x(1,t).$$

Introducing $(S, u, w) = \exp(\lambda t)(\bar{S}(x), \bar{u}(x), \bar{w}(x))$ into Eq. (4.1), we arrive at the eigenvalue problem relevant for the stability of the washout steady state,

$$\begin{aligned}\lambda\bar{S} &= d_0\bar{S}'' - \bar{S}' - \bar{u}f(1) - \epsilon\bar{w}f_w(1),\\ \lambda\bar{u} &= D\bar{u}'' - u' + \bar{u}(f(1) - k) + \epsilon\bar{w}f_w(1)(1 - G(0))\\ &\quad - \alpha\bar{u} + \epsilon\beta\bar{w},\\ \lambda\bar{w} &= d_1\bar{w}'' + \bar{w}(f_w(1)G(0) - k_w - \beta) + \epsilon^{-1}\alpha\bar{u},\end{aligned} \tag{4.2}$$

with

$$\begin{aligned}0 &= -d_0\bar{S}'(0) + \bar{S}(0), \qquad \bar{S}'(1) = 0,\\ 0 &= -D\bar{u}'(0) + \bar{u}(0), \qquad \bar{u}'(1) = 0,\\ 0 &= \bar{w}'(0) = \bar{w}'(1).\end{aligned} \tag{4.3}$$

THEOREM 4.1. *There exists a dominant real eigenvalue* Λ *of Eq.* (4.2). *That is,* $\Re\lambda < \Lambda$ *for all other eigenvalues* λ *of Eq.* (4.2). *The washout steady state is asymptotically stable if* $\Lambda < 0$ *and unstable if* $\Lambda > 0$. *If the dominant eigenvalue* $\Lambda \geq 0$, *then there is an eigenfunction* $(\bar{S}, \bar{u}, \bar{w})$ *satisfying*

$$0 < \bar{u}(x), \qquad 0 < \bar{w}(x), \qquad \bar{S}(x) < 0.$$

Proof. We note that if either $\bar{u} = 0$ or $\bar{w} = 0$, then both vanish identically. If both are zero, then we are left with Eq. (3.2) with $d = d_0$ and hence $\{\lambda_n(d_0)\}_{n\geq 0}$ are (negative) eigenvalues of Eq. (4.2). Observe that the last two equations of Eq. (4.2) are independent of $\bar{S}$. This subsystem is quasimonotone (see [16, Chap. 7] and consequently [16, Theorem 7.6.1], it has a dominant eigenvalue which we label Γ and the corresponding eigenfunction can be chosen so $(\bar{u}, \bar{w}) \gg 0$. If $\leq \lambda_0(d_0)$, then it follows that $\lambda_0(d_0) = -\lambda_{d_0}$ is the dominant eigenvalue of Eq. (4.2). If $\Gamma > \lambda_0(d_0)$, then the first equation of Eq. (4.2) is

$$-d_0\bar{S}'' + \bar{S}' + \Gamma\bar{S} = -f(1)\bar{u} - \epsilon f_w(1)\bar{w}.$$

As Γ is not an eigenvalue of the homogeneous equation, $\bar{S}$ is uniquely determined. In fact,

$$\bar{S} = -\int_0^1 G(x,\eta)\left[f(1)\bar{u} + \epsilon f_w(1)\bar{w}\right] d\eta < 0,$$

where $G > 0$ is the Green's function (see, e.g., [1, Theorem 4.4]). It follows that $\Lambda = \Gamma$ is dominant for Eq. (4.2) when $\Gamma > \lambda_0(d_0)$.

The stability assertions follow from [15, Theorem 6.1 and Theorem 4.1]. ∎

We can estimate the value of Λ. Let

$$\Delta = f_w(1)G(0) - k_w - \beta;$$

recall that Γ is the dominant eigenvalue of the eigenvalue problem consisting of the last two equations of Eq. (4.2) and $\lambda_0(d_0) < 0$ is the dominant eigenvalue of Eq. (3.2) with $d = d_0$. Then we have the following.

COROLLARY 4.2. *If $\Gamma > \lambda_0(d_0)$ (in particular, if $\Delta > \lambda_0(d_0)$), then the dominant eigenvalue Λ satisfies*

$$\Delta < \Lambda = \Gamma < s(A), \tag{4.4}$$

where $s(A)$ is the dominant eigenvalue (both are real) of

$$A = \begin{pmatrix} f(1) - k - \alpha & \alpha \\ f_w(1)(1 - G(0)) + \beta & \Delta \end{pmatrix}. \tag{4.5}$$

If $\Gamma \le \lambda_0(d_0)$, then $\Lambda = \lambda_0(d_0)$. In particular, $\Lambda > 0$ if $\Gamma > 0$ (e.g., if $\Delta \ge 0$) and $\Lambda < 0$ if $s(A) \le 0$.

Proof. Putting $\lambda = \Gamma$, $u = \bar{u}$, and $w = \bar{w}$ into the third equation and integrating, we obtain

$$[\Gamma - \Delta]\int_0^1 \bar{w} = \epsilon^{-1}\alpha\int_0^1 \bar{u} < 0.$$

As $0 < \bar{u}, \bar{w}$, we have that $\Delta < \Gamma$. Hence, according to the proof of Theorem 4.1, our first hypothesis implies that $\Lambda = \Gamma$, the dominant eigenvalue of the last two equations of Eq. (4.2). Thus, $\Delta < \Lambda$.

Now put $\lambda = \Lambda$ into the last two equations of Eq. (4.2) and integrate to get

$$\Lambda \int_0^1 \bar{u} = -\bar{u}(1) + (f(1) - k - \alpha) \int_0^1 \bar{u}$$
$$+ [f_w(1)(1 - G(0)) + \beta] \epsilon \int_0^1 \bar{w},$$

$$\Lambda \int_0^1 \bar{w} = \alpha \epsilon^{-1} \int_0^1 \bar{u} + \Delta \int_0^1 \bar{w}.$$

Letting $x = (\int_0^1 \bar{u}, \epsilon \int_0^1 \bar{w})^T$ and noting that $\bar{u}(1) > 0$, we can write this as

$$\Lambda x < A^T x,$$

where $x \gg 0$. (Here, $a < b$ means $a \le b$ and $a \ne b$ and $a \ll b$ means $a_i < b_i$ for $i = 1, 2$). This implies that $s(A) > \Lambda$. Indeed,

$$(\Lambda + r) x < (A^T + rI) x \equiv A_r x$$

for large $r > 0$ implies $\Lambda + r < \rho(A_r)$ by [5, Theorem 1.11]. Here, $\rho(A_r)$ denotes the spectral radius of the positive irreducible matrix A_r. Clearly, $\rho(A_r) = s(A_r)$ for large r and $s(A_r) = s(A) + r$.

The final conclusion was noted in the proof of Theorem 4.1. ▮

In [4], the system Eqs. (2.4)–(2.6) was considered but with immobile wall-attached bacteria, i.e., with $d_1 = 0$. In this case, the washout steady state was stable or unstable as $s(\hat{A}) < 0$ or $s(\hat{A}) > 0$, where $\hat{A}$ is the matrix

$$\hat{A} = \begin{pmatrix} f(1) - k - \alpha - \lambda_d & \alpha \\ f_w(1)(1 - G(0)) + \beta & \Delta \end{pmatrix}. \tag{4.6}$$

We might expect that $\Gamma \to s(\hat{A})$ as $d_1 \to 0$. The following result is the best we can do in this direction. However, note that $s(A_1) \to s(\hat{A})$ as $d_1 \to 0$.

PROPOSITION 4.3. *The inequality*

$$s(A_1) < \Gamma < s(A_2)$$

holds, where

$$A_1 = \begin{pmatrix} f(1) - k - \alpha - \lambda_d & \alpha \\ f_w(1)(1 - G(0)) + \beta & \Delta - (d_1/d)\lambda_d \end{pmatrix} \tag{4.7}$$

and

$$A_2 = \begin{pmatrix} f(1) - k - \alpha - \lambda_d & \alpha/\psi_d(1) \\ f_w(1)(1 - G(0)) + \beta & \Delta \end{pmatrix}, \tag{4.8}$$

where $\psi_d > 0$ *is the principal eigenfunction of Eq.* (3.3) *normalized so that* $\psi_d(0) = 1$.

Proof. We proceed as in the proof of Corollary 4.2 except that we multiply $\bar{u}$ and $\bar{w}$ by $\psi = \psi_d$ before integrating

$$\Gamma\int_0^1 \bar{u}\psi = (f(1) - k - \alpha - \lambda_d)\int_0^1 \bar{u}\psi + [f_w(1)(1 - G(0)) + \beta]\epsilon\int_0^1 \bar{w}\psi,$$

$$\Gamma\int_0^1 \bar{w}\psi = d_1\int_0^1 \bar{w}''\psi + \alpha\epsilon^{-1}\int_0^1 \bar{u}\psi + \Delta\int_0^1 \bar{w}\psi.$$

Integrating by parts and using the equation and boundary conditions satisfies by ψ yields

$$\begin{aligned}\int_0^1 \bar{w}''\psi &= -\psi'(1)\bar{w}(1) - \frac{1}{d}\int_0^1 \bar{w}\psi' - \frac{1}{d}\lambda_d\int_0^1 \bar{w}\psi \\ &\geq -\frac{\lambda_d}{d}\int_0^1 \bar{w}\psi,\end{aligned}$$

where the last inequality follows because $\psi > 0$ and

$$\psi'(x) = -\frac{\lambda_d}{d}\int_0^x e^{-(x-\eta)/d}\psi(\eta)\, d\eta < 0.$$

We get the estimate

$$\Gamma x > A_1^T x,$$

where $x = (\int_0^1 \bar{u}\psi, \epsilon\int_0^1 \bar{w}\psi) \gg 0$. Arguing as in Corollary 4.2 using [5, Theorem 1.11], we conclude that $s(A_1) < \Gamma$ (A is irreducible.

The other inequality comes about by proceeding as above except that this time, the $\bar{u}$ equation is multiplied by ψ but not the $\bar{w}$ equation, before integrating. Then, we get

$$\Gamma\int_0^1 \bar{u}\psi = (f(1) - k - \alpha - \lambda_d)\int_0^1 \bar{u}\psi + [f_w(1)(1 - G(0)) + \beta]\epsilon\int_0^1 \bar{w}\psi,$$

$$\Gamma\int_0^1 \bar{w} = \alpha\epsilon^{-1}\int_0^1 \bar{u} + \Delta\int_0^1 \bar{w}.$$

As $0 < \psi(1) \leq \psi(x) \leq \psi(0) = 1$, we can estimate as follows.

$$\Gamma\int_0^1 \bar{u}\psi < (f(1) - k - \alpha - \lambda_d)\int_0^1 \bar{u}\psi + [f_w(1)(1 - G(0)) + \beta]\epsilon\int_0^1 \bar{w},$$

$$\Gamma\int_0^1 \bar{w} < \alpha/\omega(1)\epsilon^{-1}\int_0^1 \bar{u}\psi + \Delta\int_0^1 \bar{w}.$$

The remainder of the argument follows as in the case above. ∎

We are able to show that the washout steady state is globally attracting when a stronger assumption than $\Lambda < 0$ is assumed.

PROPOSITION 4.4. *If $s(B)$, the dominant eigenvalue of matrix*

$$B = \begin{pmatrix} f(1) - k & \alpha \\ f_w(1) + \beta & \Delta \end{pmatrix}, \tag{4.9}$$

satisfies $s(B) < 0$, then

$$(u(x,t), w(x,t)) \to 0, \qquad t \to \infty,$$

uniformly in $x \in [0, 1]$.

Proof. Choose $\delta > 0$ such that $s(B_\delta) < 0$, where B_δ differs from B in that $1 + \delta$ replaces 1 in the argument of f and f_w. As $S(x,t) < 1 + \delta$ for all large t, say $t > T$, we have the inequalities

$$u_t \le du_{xx} - u_x + u(f(1+\delta) - k) + \epsilon w[f_w(1+\delta) + \beta],$$

$$w_t \le d_1 w_{xx} + [f_w(1+\delta)G(0) - k_w - \beta]w + \epsilon^{-1}\alpha u.$$

By a standard comparison argument for quasimonotone systems (see [16, Theorem 7.3.4], we have the estimate $u(x,t) \le \hat{u}(x,t)$ and $w(x,t) \le \hat{w}(x,t)$ for $t > T$, where $(\hat{u}, \hat{w})$ is the solution of the linear parabolic differential equality with initial data $(u(x,T), w(x,T))$. If the principal eigenvalue Γ^* of the eigenvalue problem

$$\lambda u = du'' - u' + u(f(1+\delta) - k) + \epsilon w[f_w(1+\delta) + \beta],$$

$$\lambda w = d_1 w'' + [f_w(1+\delta)G(0) - k_w - \beta]w + \epsilon^{-1}\alpha u,$$

is negative, then we are done. But the arguments used in Proposition 4.2 and our hypothesis imply that $\Gamma^* < 0$. ∎

Remark 4.1. The conclusion of Proposition 4.4 holds if the weaker condition $\Gamma^* < 0$ holds. Note that $s(A) < s(B)$ since $A < B$ (by direct computation or see [5]).

5. PERSISTENCE AND EXISTENCE OF A POPULATION STEADY STATE

When either the washout steady state is unstable or when it does not exist because bacteria are present in the feed ($u^0 > 0$), one may expect the bacterial population could survive in the reactor. In order to confirm this, we will prove the uniform persistence of the population and the existence of a coexistence steady state for the model system Eqs. (2.4)–(2.5). We start with the following two lemmas.

LEMMA 5.1. *For any* $(S_0, u_0, w_0) \in X$ *with at least one of* u_0 *and* w_0 *being not zero identically, the solution* $(S(x,t), u(x,t), w(x,t))$ *of Eqs.* (2.4)–(2.6) *satisfies*

$$S(x,t) > 0, \qquad u(x,t) > 0, \quad \textit{and} \quad w(x,t) > 0, \qquad \textit{for all } x \in [0,1] \textit{ and } t > 0.$$

Proof. By Proposition 3.1, we have $S(x,t) \geq 0$, $u(x,t) \geq 0$, $w(x,t) \geq 0$, $x \in [0,1]$, $t \geq 0$. Let

$$a(x,t) := u(x,t)g(S(x,t)) + \epsilon w(x,t)g_w(S(x,t)), \qquad x \in [0,1], \quad t \geq 0,$$

where $g(S) = \frac{f(S)}{S}$ is $S > 0$ and $g(0) = f'(0)$ and similarly for g_w. Note both g and g_w are continuous. By Eqs. (2.4)–(2.5), $S(x,t)$ solves the following linear nonautonomous parabolic equation

$$S_t = d_0 S_{xx} - S_x - a(x,t)S, \qquad x \in (0,1), \quad t > 0, \tag{5.1}$$

with boundary condition

$$-d_0 S_x(0,t) + S(0,t) = 1, \qquad S_x(1,t) = 0, \quad t > 0. \tag{5.2}$$

By the parabolic maximum principle (see, e.g., [19, Theorems 9.6 and 9.12], it then follows that $S(x,t) > 0$ for all $x \in [0,1]$, $t > 0$. For any $(x,t) \in [0,1] \times [0,\infty)$, we define a matrix-valued function $M(x,t) :=$

$$\begin{pmatrix} f(S(x,t)) - k - \alpha & \epsilon f_w(S(x,t))(1 - G(w(x,t))) + \epsilon\beta + \alpha u(x,t) \\ \epsilon^{-1}\alpha & f_w(S(x,t))G(w(x,t)) - k_w - \beta - \epsilon^{-1}\alpha u(x,t) \end{pmatrix}.$$

Thus from Eqs. (2.4)–(2.5), it follows that $(u(x,t), w(x,t))$ satisfies the following weakly coupled nonautonomous parabolic system

$$\frac{\partial}{\partial t}\begin{pmatrix} u \\ w \end{pmatrix} = \begin{pmatrix} d\dfrac{\partial^2}{\partial x^2} - \dfrac{\partial}{\partial x} & 0 \\ 0 & d_1\dfrac{\partial^2}{\partial x^2} \end{pmatrix}\begin{pmatrix} u \\ w \end{pmatrix} + M(x,t)\begin{pmatrix} u \\ w \end{pmatrix}, \qquad x \in (0,1), \quad t > 0. \tag{5.3}$$

with boundary conditions

$$\begin{aligned} -du_x(0,t) + u(0,t) &= u^0, \qquad u_x(1,t) = 0, \quad t > 0, \\ w_x(0,t) &= w_x(1,t) = 0, \quad t > 0. \end{aligned} \tag{5.4}$$

Clearly, we have

$$u_t \geq du_{xx} - u_x + \left[f(S(x,t)) - k - \alpha \right] u, \qquad x \in (0,1), \quad t > 0,$$

and

$$w_t \geq d_1 w_{xx} + \left[f_w(S(x,t)) G(w(x,t)) - k_w - \beta - \epsilon^{-1} \alpha u(x,t) \right] w, \qquad x \in (0,1), \quad t > 0.$$

Since at least one of $u_0(\cdot)$ and $w_0(\cdot)$ is not zero identically, the maximum principle of scalar parabolic equations implies that at least one of $u(x,t)$ and $w(x,t)$ is positive for all $x \in [0,1]$ and $t > 0$. The matrix $M(x,t)$ is cooperative and irreducible for any $(x,t) \in [0,1] \times (0,\infty)$. By the maximum principle of parabolic systems (see, e.g., [16, Theorem 7.2.5 and the proof of Theorem 7.4.1]), it then follows that $u(x,t) > 0$ and $w(x,t) > 0$ for all $x \in [0,1]$ and $t > 0$. ∎

Remark 5.1. In the case that $u^0 > 0$, it is easy to see from the above proof that the conclusion of Lemma 5.1 holds for any initial function $(S_0, u_0, w_0) \in X$.

LEMMA 5.2. *Let $u^0 = 0$ and assume that $\Lambda > 0$ (which implies $\Lambda = \Gamma$). Then there exists a $\delta_0 > 0$ such that for any $(S_0, u_0, w_0) \in X$ with at least one of $u_0(\cdot)$ and $w_0(\cdot)$ being not zero identically, the soloution $(S(x,t), u(x,t), w(x,t))$ of Eqs.* (2.4)–(2.6) *satisfies*

$$\limsup_{t \to \infty} \| (S(\cdot,t), u(\cdot,t), w(\cdot,t)) - (1,0,0) \|_\infty \geq \delta_0.$$

Proof. Let M_0 be the coefficient matrix with respect to $\bar{u}$ and $\bar{w}$ in the reaction terms of the last two equations of Eq. (4.2). Since $\Gamma > 0$, by the continuity of principal eigenvalue, we can choose a small real number $m > 0$ such that the principal eigenvalue, $\Gamma(m)$, of the coupled elliptic system

$$\lambda \begin{pmatrix} u \\ w \end{pmatrix} = \begin{pmatrix} d\dfrac{\partial^2}{\partial x^2} - \dfrac{\partial}{\partial x} & 0 \\ 0 & d_1 \dfrac{\partial^2}{\partial x^2} \end{pmatrix} \begin{pmatrix} u \\ w \end{pmatrix} + \left(M_0 - m \begin{pmatrix} 1 & 1 \\ 0 & 1 \end{pmatrix} \right) \begin{pmatrix} u \\ w \end{pmatrix} \tag{5.5}$$

with boundary conditions

$$-du_x(0) + u(0) = 0,\ u_x(1) = 0, \qquad w_x(0) = w_x(1) = 0, \tag{5.6}$$

is positive. Let $(\tilde{u}, \tilde{w})$ be the eigenfunction associated with $\Gamma(m)$. Then $\tilde{u}(x) > 0$ and $\tilde{w}(x) > 0$ for all $x \in [0,1]$. For any $(S, u, w) \in R^+ \times R^+ \times [0,1]$, we define the matrix-valued function

$$F(S,u,w) := \begin{pmatrix} f(S) - k - \alpha & \epsilon f_w(S)(1 - G(w)) + \epsilon\beta + \alpha u \\ \epsilon^{-1}\alpha & f_w(S)G(w) - k_w - \beta - \epsilon^{-1}\alpha u \end{pmatrix}.$$

Since $\lim_{(S,u,w)\to(1,0,0)} F(S,u,w) = M_0$, there exists a $\delta_0 > 0$ such that for any $(S,u,w) \in R^+ \times R^+ \times [0,1]$ with $|(S,u,w) - (1,0,0)| < \delta_0$,

$$F(S,u,w) \geq M_0 - m\begin{pmatrix} 1 & 1 \\ 0 & 1 \end{pmatrix}. \tag{5.7}$$

Suppose that, by contradiction, there exists some $(S_0, u_0, w_0) \in X$ with at least one of $u_0(\cdot)$ and $w_0(\cdot)$ being not zero identically such that

$$\limsup_{t\to\infty} \| S(\cdot,t), u(\cdot,t), w(\cdot,t) - (1,0,0) \|_\infty < \delta_0.$$

Then there exists $t_0 > 0$ such that

$$\|(S(\cdot,t), u(\cdot,t), w(\cdot,t)) - (1,0,0)\|_\infty < \delta_0, \qquad \text{for all } t \geq t_0, \tag{5.8}$$

and hence, by Eq. (5.7), we have

$$F(S(x,t), u(x,t), w(x,t)) \geq M_0 - m\begin{pmatrix} 1 & 1 \\ 0 & 1 \end{pmatrix}, \qquad x \in [0,1], \quad t \geq t_0. \tag{5.9}$$

Thus $(u(x,t), w(x,t))$ satisfies

$$\frac{\partial}{\partial t}\begin{pmatrix} u \\ w \end{pmatrix} \geq \begin{pmatrix} d\dfrac{\partial^2}{\partial x^2} - \dfrac{\partial}{\partial x} & 0 \\ 0 & d_1\dfrac{\partial^2}{\partial x^2} \end{pmatrix}\begin{pmatrix} u \\ w \end{pmatrix} + \left(M_0 - m\begin{pmatrix} 1 & 1 \\ 0 & 1 \end{pmatrix}\right)\begin{pmatrix} u \\ w \end{pmatrix}, \qquad x \in (0,1), \quad t \geq t_0. \tag{5.10}$$

Since $(u(t_0), w(t_0)) \gg 0$ and $(\tilde{u}, \tilde{w}) \gg 0$ in $C([0,1], R) \times C([0,1], R)$, there exists a real number $k > 0$ such that

$$\left(u(x,t_0), w(x,t_0)\right) \geq k\left(\tilde{u}(x), \tilde{w}(x)\right), \qquad x \in [0,1].$$

By the standard comparison theorem of quasimonotone parabolic systems, it then follows that

$$\begin{pmatrix} u(x,t) \\ w(x,t) \end{pmatrix} \geq k e^{\Gamma(m)(t-t_0)} \begin{pmatrix} \tilde{u}(x) \\ \tilde{w}(x) \end{pmatrix}, \qquad x \in [0,1], \quad t \geq t_0, \quad (5.11)$$

which contradicts Eq. (5.8) when we let $t \to \infty$. ∎

Now we are in a position to prove the main results in this section.

THEOREM 5.1. *Assume that* $u^0 = 0$ *and* $\Lambda > 0$. *Then system of Eqs.* (2.4)–(2.6) *admits at least one componentwise positive steady state and is uniformly persistent in the sense that there exists a real number* $\eta > 0$ *such that for any* $(S_0, u_0, w_0) \in X$ *with at least one of* $u_0(\cdot)$ *and* $w_0(\cdot)$ *being not zero identically, there exists a* $T_0 = T_0(S_0, u_0, w_0) > 0$ *such that the solution* $(S(x,t), u(x,t), w(x,t))$ *of Eqs.* (2.4)–(2.6) *satisfies*

$$S(x,t) \geq \eta, \qquad u(x,t) \geq \eta, \qquad w(x,t) \geq \eta, \qquad x \in [0,1], \quad t \geq T_0.$$

Proof. Let $\Phi(t)$: $X \to X$, $t \geq 0$, be the solution semiflow induced by Eqs. (2.4)–(2.6). Then $\Phi(t)$ is compact for each $t > 0$ and Φ has a global attractor in X by Theorem 3.2. Let

$$X_0 = \left\{(S_0, u_0, w_0) \in X;\ S_0(\cdot) \not\equiv 0,\ u_0(\cdot) \not\equiv 0,\ w_0(\cdot) \not\equiv 0\right\}$$
$$\text{and} \quad \partial X_0 = X \setminus X_0.$$

Then, by Lemma 5.1, $\Phi(t)X_0 \subset X_0$, $t \geq 0$. For any $(S_0, u_0, w_0) \in X$ with $u_0(\cdot) \equiv 0$ and $w_0(\cdot) \equiv 0$, we have $u(x,t) \equiv 0$ and $w(x,t) \equiv 0$ for $x \in [0,1]$ and $t \geq 0$, and hence $S(x,t)$ satisfies

$$\begin{aligned} S_t &= d_0 S_{xx} - S_x, & x \in (0,1), \quad t > 0, \\ -d_0 S_x(0,t) + S(0,t) &= 1, & S_x(1,t) = 0, \quad t > 0. \end{aligned} \qquad (5.12)$$

As noted in Section 3, we have $\lim_{t \to \infty} S(x,t) = 1$ uniformly for $x \in [0,1]$, and hence

$$\lim_{t \to \infty} \left\|(S(\cdot,t), u(\cdot,t), w(\cdot,t)) - (1,0,0)\right\|_\infty = 0.$$

By Lemma 5.1, it then follows that $(1,0,0)$ is the maximal compact isolated invariant set for $\Phi(t)$ in ∂X_0. Moreover, Lemma 5.2 implies that $(1,0,0)$ is also isolated in X_0 and is a weak repeller for X_0. By [20, Theorem 4.6], $\Phi(t)$: $X \to X$, $t \geq 0$, is uniformly persistent with respect to X_0, that is, there exists a $\delta > 0$ such that for any $(S_0, u_0, w_0) \in X_0$,

$$\liminf_{t\to\infty} d\big(\Phi(t)(S_0, u_0, w_0), \partial X_0\big) > \delta,$$

where $d(z, K)$ denotes the distance from point z to set K. Therefore, by [21, Theorem 2.4], there exists a $(S^*, u^*, w^*) \in X_0$ such that $(S^*, u^*, w^*) = \Phi(t)(S^*, u^*, w^*)$ for all $t \geq 0$. Consequently, by Lemma 5.1, (S^*, u^*, w^*) is a componentwise positive steady state of Eqs. (2.4)–(2.5). Let $Z = C([0,1], R) \times C([0,1], R) \times C([0,1], R)$ and let $e = (1,1,1)$. Clearly, $e \in int(Z^+)$. By Lemma 5.1, $\Phi(t)X_0 \subset int(Z^+)$ for any $t > 0$. Then the estimates of S, u, w from below (termed "robust persistence") follow from Theorem A.2 in the Appendix.

THEOREM 5.2. *Assume that* $u^0 > 0$. *Then system Eqs*. (2.4)–(2.6) *admits at least one componentwise positive steady state and is uniformly persistent in the sense that there exists a real number* $\eta > 0$ *such that for any* $(S_0, u_0, w_0) \in X$, *there exists a* $T_0 = T_0(S_0, u_0, w_0) > 0$ *such that the solution* $(S(x,t), u(x,t), w(x,t))$ *of Eqs*. (2.4)–(2.6) *satisfies*

$$S(x,t) \geq \eta, \qquad u(x,t) \geq \eta, \qquad w(x,t) \geq \eta, \qquad x \in [0,1], \quad t \geq T_0.$$

Proof. By Theorem 3.2, the solution semiflow $\Phi(t)$ of Eqs. (2.4)–(2.6) is dissipative and $\Phi(t)$: $X \to X$ is compact for each $t > 0$. By [9, Theorem 3.4.8] the global attractor A contains an equilibrium point $(S^*, u^*, w^*) = \Phi(t)(S^*, u^*, w^*)$ for all $t \geq 0$, and hence, by Lemma 5.1 and Remark 5.1, (S^*, u^*, w^*) is a componentwise positive steady state of Eqs. (2.4)–(2.5). Let $Z = C([0,1], R) \times C([0,1], R) \times C([0,1], R)$ and let $e = (1,1,1)$. Clearly, $e \in int(Z^+)$. Again by Lemma 5.1 and Remark 5.1, $\Phi(t)X \subset int(Z^+)$ for any $t > 0$. Then the robust persistence follows from Theorem A.1 in the Appendix. ∎

APPENDIX
ROBUST PERSISTENCE

DEFINITION A.1. Let (X, P) be an ordered Banach space with its cone P having nonempty interior $int(P)$. For two subsets A and B of X, we define $A + B = \{x + y;\ x \in A,\ y \in B\}$ and say that

(i) $A \geq B$ if $x - y \in P$ for any $x \in A$ and $y \in B$.

(ii) $A > B$ if $x - y \in P \setminus \{0\}$ for any $x \in A$ and $y \in B$.

(iii) $A \gg B$ if $x - y \in int(P)$ for any $x \in A$ and $y \in B$.

THEOREM A.1. *Let X_0 be a metric space, let (Z, Z^+) be an ordered Banach space with $int(Z^+) \neq \emptyset$ and let $S(t)$: $X_0 \to X_0$, $t \geq 0$, be an autonomous semiflow. Assume that*

(A1) $S(t)$ has a global attractor A_0 in X_0 in the sense that A_0 is a compact and invariant subset of X_0 and A_0 attracts every point in X.

(A2) There exists a $t_0 > 0$ such that $S(t_0)X_0 \subset int(Z^+)$ and $S(t_0)$: $X_0 \to int(Z^+)$ is continuous.

Then for any given $e \in int(Z^+)$, there exists a $\beta > 0$ such that for any $x \in X_0$, there exists a $T_0 = T_0(x) \geq t_0$ such that

$$S(t)x \geq \beta e \text{ in } Z, \quad \text{for all } t \geq T_0.$$

Proof. Clearly, the semigroup property of $S(t)$ and assumption (A2) of Theorem A.1 imply that $S(t)X_0 \subset int(Z^+)$ for any $t \geq t_0$. By the compactness and invariance of A_0 and the continuity of $S(t_0)$: $X_0 \to int(Z^+)$, it then follows that $A_0 = S(t_0)A_0$ is also a compact subset of $int(Z^+)$ in Z. Then for every $x \in A_0$, there is a $\beta_x > 0$ such that $x \gg \beta_x e$ in Z. Since $x - \beta_x e \in int(Z^+)$, there exists an open subset V_x of Z such that $x - \beta_x e \in V_x \subset int(Z^+)$. Then $W_x = \beta_x e + V_x$ is and open neighborhood of x in Z, and $y \gg \beta_x e$ for every $y \in W_x$. Clearly, $\bigcup_{x \in A_0} W_x$ is an open cover of A_0. By the compactness of A_0 in Z, there exist an open subset $W = W(A_0)$ fo Z and a $\beta = \beta(A_0) > 0$ such that $A_0 \subset W$ and $W \gg \beta e$ in Z.

For any $x \in X_0$, $S(t)x \to A_0$ in X_0 as $t \to \infty$, and hence, again by the continuity of $S(t_0)$: $X_0 \to Z$, we get $S(t_0)(S(t)x) \to S(t_0)A_0 = A_0$ in Z as $t \to \infty$. It then follows that there exists a $t_1 = t_1(x) > 0$ such that $S(t_0)(S(t)x) \in W$ for all $t \geq t_1$, and hence

$$S(t + t_0)x = S(t_0)(S(t)x) \gg \beta e \text{ in } Z, \quad \text{for all } t \geq t_1.$$

On letting $T_0 = t_1(x) + t_0$, we complete the proof. ∎

DEFINITION A.2. Let (X, d) be a complete metric space with metric d, and let X_0 and ∂X_0 be open and closed subsets of X, respectively, such that $X_0 \cap \partial X_0 = \emptyset$ and $X = X_0 \cup \partial X_0$. A subset B of X_0 is said to be strongly bounded if B is bounded and $d(B, \partial X_0) = \inf_{x \in B} d(x, \partial X_0) > 0$. An autonomous semiflow $S(t)$: $X \to X$ with $S(t)X_0 \subset X_0$, $t \geq 0$, is said to be uniformly persistent with respect to $(X_0, \partial X_0)$ if there exists an $\eta > 0$ such that for any $x \in X_0$, $\liminf_{t \to \infty} d(S(t)x, \partial X_0) \geq \eta$.

THEOREM A.2. *Let X, X_0, ∂X_0 be as in Definition A.2, let (Z, Z^+) be an ordered Banach space with $int(Z^+) \neq \emptyset$, and let $S(t)$: $X \to X$, $t \geq 0$, be an autonomous semiflow with $S(t)X_0 \subset X_0$, $t \geq 0$. Assume that*

(C1) $S(t)$: $X \to X$ is point dissipative, compact for $t \geq t_1 > 0$, and is uniformly persistent with respect to $(X_0, \partial X_0)$.

(*C*2) *There exists a* $t_2 > 0$ *such that* $S(t_2)X_0 \subset int(Z^+)$ *and* $S(t_2)$: $X_0 \to int(Z^+)$ *is continuous.*

Then for any given $e \in int(Z^+)$, *there exists a* $\beta > 0$ *such that for any strongly bounded subset B of* X_0, *there exist a* $T_0 = T_0(B) \geq t_2$ *such that*

$$S(t)B \geq \beta e \text{ in } Z, \qquad \text{for all } t \geq T_0.$$

Proof. By condition (C1) and an argument similar to that in [10, Theorems 3.2 and 3.3], it follows that $S(t)$: $X_0 \to X_0$ has a global attractor A_0 which attracts every strongly bounded subset of X_0. Now the assertion follows from the argument given in the second part of the proof of Theorem A.1 with x replaced by B.

Remark A.1. For a scalar reaction-diffusion equation, by setting $X = C^+(\overline{\Omega}, R)$, $Z = C(\overline{\Omega}, R)$, and $e = 1 \in int(Z^+)$ in the Neumann or Robin type of boundary condition and setting $X = C_0^+(\overline{\Omega}, R)$, $Z = C_0^1(\overline{\Omega}, R)$, and $e \in int(Z^+)$ in the Dirichlet boundary condition, by Theorem A.2, we can get the robust persistence from the uniform persistence of the semiflow $\Phi(t)$ on X generated by the reaction-diffusion equation. This is because of the fact that for any $t > 0$, $\Phi(t)$: $X \to Z$ is continuous in the case of Dirichlet boundary condition (see [16, proof of Corollary 7.4.2]). A similar remark applies to reaction-diffusion systems.

Remark A.2. For a functional differential equation on $C([-r, 0), R)$, one can set $X = C^+([-r, 0], R)$, $Z = C([-r, 0], R)$, and $e = 1 \in int(Z^+)$ in order to get robust persistence. Combining Remark A.1, one can also easily figure out the choices for reaction-diffusion systems with delays.

Remark A.3. For reaction-diffusion equations, one could expect another kind of robust persistence in the sense that there exists a $\beta_0 > 0$ such that for any $\phi \in X_0$, there exists a $T_0 = T_0(\phi) > 0$ such that

$$\int_\Omega u(x, t, \phi)\, dx \geq \beta_0, \qquad \text{for all } t \geq T_0.$$

Clearly, the conclusion that $u(x, t, \phi) \geq \beta e(x)$, $x \in \Omega$, $t \geq T_0$, implies that $\int_\Omega u(x, t, \phi)\, dx \geq \beta \int_\Omega e(x)\, dx = \beta_0 > 0$, for all $t \geq T_0$. Therefore, we would like to refer to the conclusion in Theorem A.1 as robust persistence.

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